Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): Insights from satellite tag tracking and remotely sensed data

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Abstract

We analyzed satellite track data for 186 loggerhead sea turtles in the North Pacific Ocean using remotely sensed environmental data to characterize pelagic habitat. A large number of candidate habitat variables were merged to the satellite track data and statistically compared to background values over a large spatiotemporal grid which bounded overall occupancy. Five statistically significant variables were identified out of the 16 environmental variables examined. Two of these variables have strong seasonal, interannual, and spatial patterns (sea surface temperature and chlorophyll *a* concentration), while three others were primarily spatial (earth magnetic force, earth magnetic declination, and earth magnetic inclination). Habitat selectivity for these variables was quantified using preference curve methodology established in the foraging literature. The output from the selectivity curves was used to predict a multivariate loggerhead sea turtle habitat index across the pelagic North Pacific. This predicted habitat was ground-truthed with newly available satellite track data.
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1. Introduction

The spatial distribution of pelagic organisms is determined by physical-forcing mechanisms (winds, waves, currents, tides, etc.) coupled with active movement processes by the organisms. Large pelagic macrofauna such as nekton (by definition) possess good swimming ability and can regulate their location actively. Despite the apparent homogeneity of the open ocean habitat, many scales of structure in the physical environment can be used by nektonic organisms to locate and maintain position in preferred habitat (Longhurst, 2006). The distribution and abundance of most studied nekton exhibit this type of patterned occupancy, i.e., they are not simply distributed randomly or uniformly throughout the open ocean. Sea turtles are one such group of nekton which displays structured pelagic distributions (Carr, 1987; Luschi et al., 2003; Polovina et al., 2000, 2006), presumably via some component of active orientation since even hatchling sea turtles possess good swimming ability (O'Hara, 1980; Davenport and

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Clough, 1986). Some species, such as leatherback sea turtles (*Dermochelys coriacea*), have been shown to have complex patterns of pelagic habitat utilization, not always related to forage or biological "hot spots" (Hays et al., 2006). Loggerhead sea turtles (*Caretta caretta*), a threatened species under the US Endangered Species Act, are capable of traversing both major ocean basins during their ontogenetic migrations (Bowen et al., 1995; Bolten et al., 1998; Alfaro-Shigueto et al., 2004). Many of these long-distance migrations are between nesting grounds and foraging grounds. Juvenile, subadult, and adult loggerhead sea turtles in the North Pacific Ocean have been shown to occupy specific areas of the pelagic environment, possibly related to sea surface temperature and/or ocean productivity (Polovina et al., 2000, 2004, 2006). Based on these and previous studies (e.g., Zug et al., 1995), it is clear that loggerhead sea turtles use some portion of the open ocean for a large fraction of their life history, yet their particular habitat requirements are largely unknown.

Habitat characterization for broad-ranging pelagic organisms has historically been hampered by a lack of complete positional data as well as a lack of biologically pertinent and synoptic environmental data. With recent advances in satellite-mediated tagging technology and accessibility to many remotely sensed environmental data products, much more information is now available on location and movement of individuals and their exposure to a wide variety of environmental variables. We have been tagging loggerhead sea turtles in the North Pacific with Argos-linked satellite tags since 1997 via the collaborative efforts of a large, multinational group of marine turtle researchers (Table 1). Both captive-reared and wild-caught individuals have been tagged and tracked. Subsets of this satellite tag dataset have been used elsewhere to examine relationships to fronts (Polovina et al., 2000), diving behavior (Polovina et al., 2003), foraging behavior (Polovina et al., 2004), and characterization of geographic "hot spots" of distribution (Polovina et al., 2006). In this paper, we use the satellite tag data coupled with remotely sensed environmental data to characterize loggerhead sea turtle pelagic habitat across the North Pacific Ocean using quantitative approaches.

2. Methods

2.1. Satellite tracking

All wild-caught (fishery bycatch or nesting individuals) and captive-reared loggerhead sea turtles tagged in this analysis are summarized in Table 1, and the track data are shown graphically in Fig. 1. Turtles were outfitted with satellite transmitters attached to the carapace using the procedures outlined in Balazs et al. (1996). Turtles were equipped with Telonics (Mesa, AZ, USA) model ST-18, ST-19, ST-24, and Wildlife Computers (Redmond, WA, USA) model SDR-T10, SDR-T16, or SPOT 3/4/5 Argos-linked satellite transmitters. Only the highest quality position data (Argos codes 0–3) were kept initially, and only one dataset from a tag was used for twelve dual-tagged turtles. A subsequent screening removed satellite fixes which predicted unlikely sustained swimming velocities, similar to the methodology of McMahon and Hays (2006), although we used a slightly larger arbitrary cutoff of 5 m/s instead of 2.5 m/s since some of the surface current speeds in this area can be ~2.5 m/s.

Environmental data grids were merged to the satellite track data using the software package Generic Mapping Tools (GMT), extending the approach of Ellis and Balazs (1998). A GMT subroutine called *grdtrack* was used to extract trackline values from the weekly or monthly gridded data fields with a spatial bicubic interpolation. Monthly data fields were used when weekly resolution resulted in excessive missing values as a result of cloud cover, sensor malfunction or missing files. The GMT software package (Wessel and Smith, 1991) is available from http://gmt.soest.hawaii.edu/ and was used for most of the gridding, mapping, and analysis of this study. Missing values affected 11.30% of the total records in the satellite track data,

Table 1
Summary of loggerhead sea turtle satellite tag deployments by major dataset grouping

Data source	Latitude$_{min}$	Latitude$_{max}$	Longitude$_{min}$	Longitude$_{max}$	Date$_{min}$	Date$_{max}$	SCL$_{min}$	SCL$_{max}$	Datapoints	Percent	Tags
Nagoya	22.54°N	45.42°N	136.60°E	144.23°W	23-Apr-2003	30-Jun-2006	25.60	64.80	41509	90.23%	110
Historical	20.94°N	41.46°N	162.30°E	131.03°W	26-Jan-1997	23-Oct-2001	41.00	83.00	5392	97.50%	30
Japan	23.77°N	39.48°N	125.15°E	164.15°E	9-Dec-2002	12-Jun-2006	66.50	89.10	2170	26.87%	15
Taiwan	3.99°N	37.75°N	108.88°E	162.31°E	10-May-2002	1-Jul-2006	64.00	83.00	1459	10.08%	18
Baja	15.69°N	35.05°N	168.03°E	108.95°W	10-Oct-1998	14-Dec-2002	54.50	77.10	725	13.10%	13

Data source	Description of data
Nagoya	"Nagoya" refers to tag and release conducted upon reared turtles by Dr. Itaru Uchida, Masanori Kurita, Tomomi Saito, and other Port of Nagoya Public Aquarium staff.
Historical	"Historical" refers to tag and release conducted upon bycatch in the Hawaii-based longline fishery by Pacific Islands Fisheries Science Center, National Marine Fisheries Service staff and fishery observers.
Japan	"Japan" refers to tag and release conducted upon nesting individuals and bycatch in the Japanese pond net fishery by Dr. Naoki Kamezaki and colleagues.
Taiwan	"Taiwan" refers to tag and release conducted upon bycatch in the Taiwanese pond net fishery by Dr. I-Jiunn Cheng and colleagues.
Baja	"Baja" refers to tag and release conducted upon bycatch in the Baja California Sur, Mexico coastal gillnet fishery by Dr. Peter Dutton and colleagues (Wallace J. Nichols, Hoyt Peckham, Jeffrey Seminoff, and The Grupo Tortuguero of Baja California).

Summary includes latitude ranges (south to north), longitude ranges (east to west), date ranges, SCL size ranges (cm straight carapace length), number of high-quality satellite data hits, percent of track data in pelagic habitat, and number of tags deployed (not counting dual-tagged individuals). Latitude, longitude, and date ranges refer to the range of values throughout the satellite tracks, from deployment through to the time of this summary (July 2006). SCL ranges refer to the size upon release and does not account for growth. A description of the data is in the lower panel of the table.
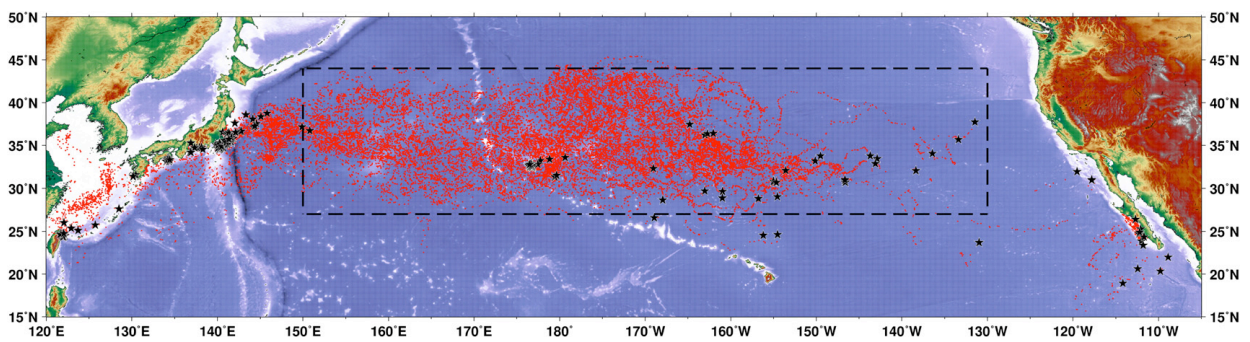
Fig. 1. Map of North Pacific Ocean and 186 satellite tagged loggerhead sea turtle locations (red) covering the time span 26 January, 1997–1 July, 2006. Dashed line delineates grid used for pelagic habitat study, 150°E–130°W longitude, 27°N–44°N latitude. Stars indicate release points for individual tracks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

primarily because of missing coverage in SST and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data.

2.2. Environmental data products

Satellite-derived chlorophyll *a* pigment concentrations were taken from the SeaWiFS instrument aboard the Seastar earth-orbiting satellite (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). The data used in this paper is chlorophyll *a* data derived from the raw measured wavelength bands (9 km, 8-day resolution) available from NASA using the SeaWiFS algorithm (SeaWiFS L3 CHLO Version 5). Regridded monthly data at 0.1° latitude/longitude data were merged to the satellite track data. Chlorophyll *a* is a likely key variable for pelagic habitat since it may be indicative of forage availability for loggerhead sea turtles (Polovina et al., 2001).

Sea surface temperature (SST) from Advanced Very High Resolution Radiometer (AVHRR) sensors aboard earth-orbiting NOAA satellites was merged to the satellite track data. The 4 km resolution Pathfinder v5.0 SST (http://www.nodc.noaa.gov/sog/pathfinder4km) is a new reanalysis of the AVHRR data stream, developed and administered by the University of Miami Rosenstiel School of Marine and Atmospheric Science, the NOAA National Oceanographic Data Center, and NASA Physical Oceanography Distributed Active Archive Center. This was regridded to 8-day 0.1° latitude/longitude data product covering 1997–2003 for this study. For SST subsequent to 2003, NOAA Global Area Coverage SST was used in place of Pathfinder SST at an identical resolution. Correspondence between these two SST datasets is very high (Evan A. Howell, pers. comm.), and for simplicity SST is henceforth referred to as Pathfinder SST. Ocean surface temperature was chosen as a candidate variable because it is known to be a strong orientation cue for sea turtles (e.g., McMahon and Hays, 2006).

An SST-related index of thermal fronts was also merged to the satellite track data. This was a weekly 0.1° latitude/longitude Pathfinder SST-gradient index, a combined N/S, E/W gradient of SST used as an indicator of thermal discontinuities. Such features may be important for pelagic habitat, since previous work has shown relationships of loggerhead sea turtles to thermal fronts (Polovina et al., 2003, 2004).

Sea surface height (SSH) and geostrophic flow fields derived from the sea surface topography were obtained from NOAA OceanWatch, Central Pacific regional node, at the Pacific Islands Fisheries Science Center (PIFSC) National Marine Fisheries Service (NMFS) (http://oceanwatch.pifsc.noaa.gov/). SSH is measured by microwave radar altimeters aboard earth-orbiting satellites Topex/POSEIDON and Jason-1. Geostrophic currents were calculated using the methodology of Polovina et al. (1999). Changes in sea surface topography are related to large-scale water mass dynamics, geostrophic flow; and, for example, 170 cm SSH is used as a marker for the Kuroshio Extension axis (Qiu and Chen, 2005), a biologically important region for loggerheads (Polovina et al., 2006).

Wind data were obtained from microwave scatterometer sensors aboard earth-orbiting satellites ERS-1, ERS-2, and QuickSCAT. Monthly data grids at a resolution of 0.1° latitude/longitude were accessed from NOAA OceanWatch, Central Pacific regional node at the PIFSC, NMFS. Wind stress components in the east–west and north–south directions were evaluated separately, as well as the total resultant wind stress vector magnitude. Wind stress is a potentially important variable for sea turtles since they are air-breathing and, therefore, epipelagic for a significant portion of their time. There may be strong wind-driven circulation in that section of the water column, and possible wind effects on the sea turtle carapace or even on the satellite transmitter unit (e.g., Watson and Granger, 1998).

Global magnetic data were calculated using the software GeoMag 6.0 available from the NOAA National Geophysical Data Center (http://www.ngdc.noaa.gov/seg/geom_util/geomutil.shtml). This software is driven by the International Geomagnetic Reference Field 10th generation (henceforth IGRF-10) coefficients. These coefficients are updated every 2–6 years by the International Association of Geomagnetism and Aeronomy and were last updated in 2005. Four magnetic variables were examined in this study: declination, inclination, total force, and orthogonality of the inclination and total force gradients. Declination is the departure between true-north and magnetic north (degrees), which is biologically relevant for the many organisms possessing simple compass-like abilities (Lohmann and Lohmann, 2006). Inclination is a measure of the direction of the total force field into the earth (degrees) and has been shown to be detectible by sea turtles (Light et al., 1993). Both declination and inclination characterize the direction of the earth's magnetic field and may be significant for pelagic orientation. Total force is a measure of the intensity of the earth's magnetic field in nanoteslas and has also been shown to be detectible by sea turtles (Lohmann and Lohmann, 1996). These three variables were output from the GeoMag 6.0 software at a monthly resolution of 0.1° latitude/longitude. The index of orthogonality was constructed to measure the degree of perpendicularity of inclination and total force axes. If these two variables have gradients at 90° or 270° of one another, this may serve as an effective Cartesian coordinate system for pelagic navigation, analogous to an $x-y$ coordinate system such as longitude and latitude. Orthogonality was calculated pixel-by-pixel using the GMT subroutines *grdgradient* to calculate the directional gradient in a grid at a particular pixel location, and *grdmath* to perform calculations on the two grids. The linear index created ranged from 0 (gradients in identical or exactly opposite directions) to 1 (gradients at 90° or 270° of one another), using simple geometric functions.

Bathymetric data, both depth and two depth gradients (N/S, E/W), were incorporated into the satellite track data. The Smith and Sandwell (1997) 2-minute resolution global database was accessed for this step of the analysis. Since sea turtles nest on land, and are neritic for some portion of their life history, it is conceivable that water depth or water depth gradients could be important habitat descriptors.

2.3. Data analyses

The satellite track data were first examined with a non-metric multidimensional scaling (NMDS) analysis. NMDS is an ordination approach that is also useful in assessing dimensionality in a dataset (McCune and Grace, 2002). Potential

groupings of the satellite tag data were investigated since this data covers a wide geographic area, different seasons of the year, and different sizes of individuals, among many other variables. Since it is known that loggerhead sea turtles occupy a relatively narrow latitudinal range in certain instances (Polovina et al., 2000), frequency distributions of this variable (latitude) were examined in the NMDS across aggregations defined by four seasons (Winter = November–January, Spring = February–April, Summer = May–July, and Autumn = August–October), six uniformly sized longitudinal bins (breakpoints at 140°E, 160°E, 180°, 160°W, and 140°W), and two size classes of individuals defined by their straight carapace lengths (SCL) on release (small ≤ 40 cm SCL, and large > 40 cm SCL). The 40 cm SCL size cutoff corresponds ecologically to the transition between the "juvenile" and subsequent "subadult" stage, whereby swimming is thought to be more important than passive rafting (Dodd, 1988), and occurs at 8–9 years of age (Zug et al., 1995). Most of the tags and track data are from juveniles, with a small number of subadults and very few adults > 70 cm SCL (Fig. 2). NMDS was chosen as the ordination technique since most of the latitudinal frequency distributions were non-symmetrical, and such distributions are not easily characterized by a single measure such as a mean or median. NMDS is an iterative, non-parametric technique and is considered the method of choice for ordination of most ecological data

(McCune and Grace, 2002). The NMDS of these 48 aggregations was accomplished using the commercial software package PC-ORD. The NMDS indicated a possible "coastal" component of the data which will be analyzed in a separate study; this study will focus on the "pelagic" aggregation of track data (Fig. 3), spanning the bounds of 150°E–130°W longitude.

Many fundamental ecological processes involve preferences made at the individual level, e.g., mate choice, foraging behavior, and habitat selection. The quantification of such preferences has received much attention from researchers (Cock, 1978; Lechowicz, 1982; Confer and Moore, 1987) and typically involves simultaneous examination of some measure of what resources an individual uses and, equally importantly, some measure of what resources are available to that individual. Many selectivity or electivity indices have been put forth, including well known approaches such as the Forage Ratio (Savage, 1931), Ivlev's Electivity Index (Ivlev, 1961), Jacob's Electivity Index (Jacobs, 1974), Linear Index (Strauss, 1979), Manly–Chesson Alpha (Manly et al., 1972; Chesson, 1978, 1983), and Relativized Electivity (Vanderploeg and Scavia, 1979). These methods were initially developed for, and have primarily dealt with, foraging studies; but these techniques have also been applied to habitat selection behavior (e.g., Morrissey and Gruber, 1993; Lukoschek and McCormick, 2001; Carreras et al., 2004; Cardona et al., 2005). Despite much literature on this topic, no single index
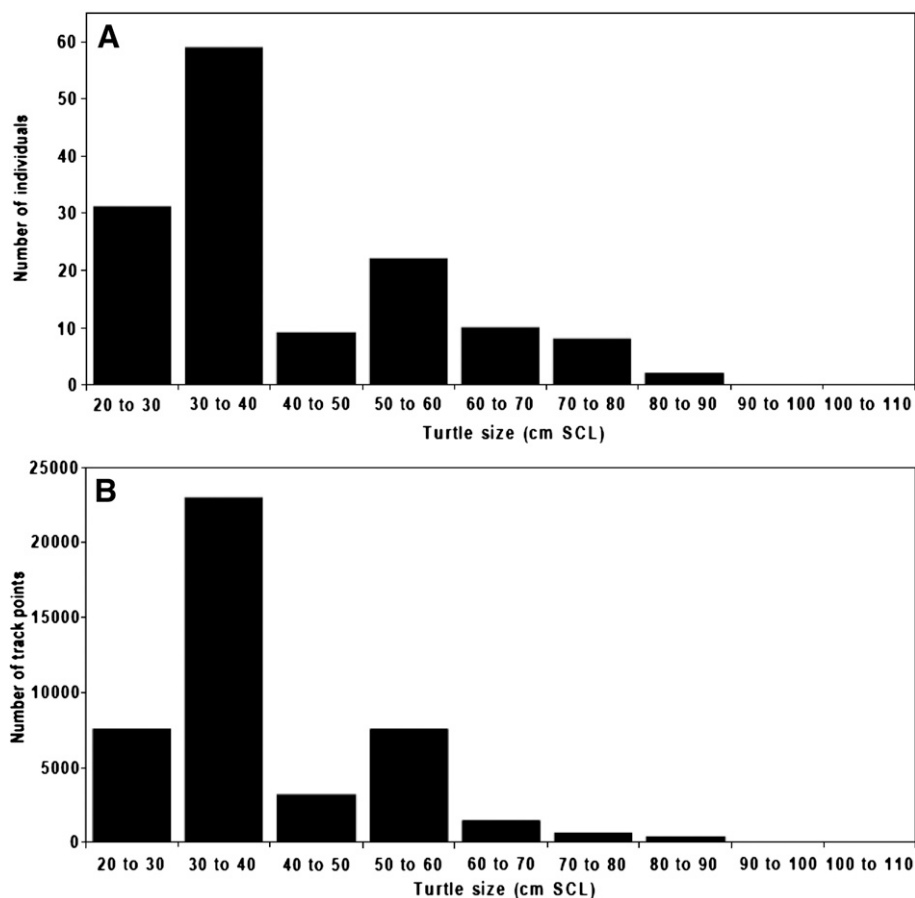

Fig. 2. Size frequency histograms of tagged loggerhead sea turtles (A.) and track data (B.) used in the analysis. Each bar represents the frequency of data in a 10 cm SCL bin.
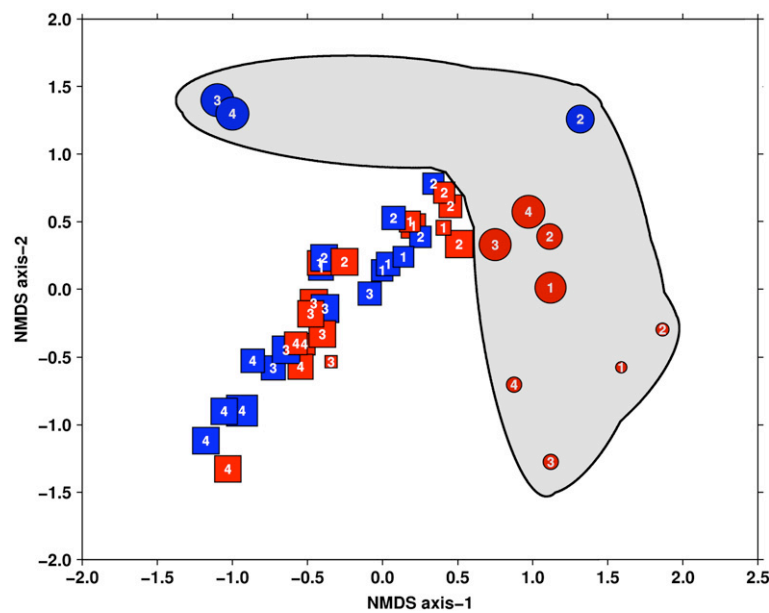
Fig. 3. Ordination results from non-metric multidimensional scaling (NMDS) analysis of latitudinal frequency distributions in the loggerhead sea turtle satellite track data. Data were aggregated into 48 data ensembles defined by unique combinations of 6 longitudinal bins, 4 seasonal bins, and 2 size-based bins. Circles represent data ensembles from the furthest east and west strata, squares represent all non-coastal data ensembles. Symbol size is proportional to mean latitude of that data ensemble (small–large symbols reflect the data range 18.5–42.8° North latitude). Blue denotes juvenile (≤ 40 cm SCL), red denotes subadult and adult (> 40 cm SCL). The number located within each symbol represents the season of that particular data ensemble (1 = winter, 2 = spring, 3 = summer, 4 = autumn). Shaded polygon denotes "coastal" pattern of farthest east and west data ensembles not addressed in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prevails. Quite often, multiple indices are calculated and contrasted (e.g., Brodeur, 1998; Govoni et al., 1986; León and Bjorndal, 2002). Lechowicz (1982) evaluated many indices and recommended Relativized Electivity, which was used by Lukoschek and McCormick (2001) to characterize goatfish habitat; the Linear Index has been used to characterize habitat in juvenile lemon sharks (Morrissey and Gruber, 1993), and the Manly–Chesson Alpha is perhaps the most widely used forage index as an alternative to the now deprecated Ivlev's Electivity Index (Cock, 1978; Chesson, 1978; Lechowicz, 1982). In this study Relativized Electivity, the Linear Index, and Manly–Chesson Alpha are applied and contrasted to characterize habitat preference in loggerhead sea turtles.

The calculation of Relativized Electivity, the Linear Index, and Manly–Chesson Alpha (henceforth designated RE, LI, and MCA, respectively) for habitat characterization requires data on the utilization (u) and availability (a) of a particular habitat variable. The subscripts i and j are added to each of the RE, LI, MCA, u, and a to indicate category i within each habitat variable j. Utilization of a particular habitat variable was simply a tabulation of values from the merged satellite track data for each of the j environmental variables into frequency distributions, after standardization these become the u_{ij}. Availability in this analysis was defined as the distribution of values available over a spatiotemporal grid encompassing the satellite track data; in other words, this is the distribution of values assumed to be available to the individual in some sequential process. After using NMDS to specify bounds of 150°E–130°W longitude, it is seen that more than 99% of the remaining satellite track data lies between 27°N and 44°N latitude. For each of the j environmental variables examined, all weekly or monthly pixel values within this

spatial grid over the January 1997–December 2006 time period were tabulated into frequency distributions of availability; after standardization these become the a_{ij}. The u_{ij} and a_{ij} were tabulated identically into N_j uniform bins representing the categories i, as input to the selectivity indices. An attempt was made to use the objective bin-size methodology of Scott (1979); however, this was unsuccessful and resulted in unworkably small bin sizes, likely based on issues related to pseudoreplication mentioned below. Bin sizes were determined qualitatively to maintain sufficient resolution so as to not obscure distributional patterns in the data.

In an approach similar to Kinzie (1988), the two cumulative frequency distributions of the raw, unbinned u_{ij} and a_{ij} were first statistically compared for each of the j habitat variables using a Kolmogorov–Smirnov (KS) test, which uses the maximum vertical distance between the two overlaid cumulative frequency distributions, referred to as $D_{\max}$ (Zar, 1984). The KS test is particularly attractive for use in habitat studies because it is sensitive to both location and shape, therefore amenable to the types of the continuous and non-symmetrical habitat variables typically encountered in biological studies (Pacheco and Henderson, 1996). The KS test was modified in two ways for this specific application. The first modification was to use a one-sample KS test to compare the u_{ij} to the a_{ij}, in a manner analogous to comparing one-sample distribution to an extrinsic and invariant distribution, e.g., comparison to a normal distribution. In this case, the comparison of u_{ij} from the tracks is made to an underlying a_{ij} distribution made up of many hundreds of thousands of background pixels of information aggregated over a large spatial grid over many years. Utilization of this large n for a_{ij} in the calculation of statistical significance is unjustified as a result of pseudoreplication (Hurlbert, 1984); i.e., this large n sampled from

the spatiotemporal grids does not reflect n independent values because of spatial correlation, pixel-based interpolation, arbitrary resolution, and temporal binning of the data. The approach taken here is to treat these background distributions a_{ij} as extrinsic and invariant. The second modification of the KS test is to similarly adjust the degrees of freedom (henceforth df) corresponding to the u_{ij} distribution. The df were conservatively adjusted to reflect the sample sizes of tagged individuals contributing to each cumulative frequency distribution, since pseudoreplication (Hurlbert, 1984) is again a potential problem, for the same reasons just described. Additionally, there is obvious lack of independence in the data as a result of many satellite "hits" along a continuous trackline coupled with the extraction of the matching environmental data from spatially and temporally discrete grids for each "hit." This adjustment of df is comparable to approaches taken elsewhere to alleviate the effects of pseudoreplication in autocorrelated datasets (Clifford et al., 1989; Pyper and Peterman, 1998). The Bonferroni correction factor was used to calculate the significant D_{max} values for $n = 16$ tests. For the N_{KS} variables which had statistically significant differences in u_{ij} and a_{ij} using the modified KS test, further analysis was performed with the preference indices RE_{ij}, LI_{ij} and MCA_{ij}, which were calculated using the following equations:

$$RE_{ij} = \frac{\dfrac{\dfrac{u_{ij}}{a_{ij}}}{\displaystyle\sum_{i=1}^{N_j}\dfrac{u_{ij}}{a_{ij}}} - \dfrac{1}{N_j}}{\dfrac{\dfrac{u_{ij}}{a_{ij}}}{\displaystyle\sum_{i=1}^{N_j}\dfrac{u_{ij}}{a_{ij}}} + \dfrac{1}{N_j}}$$

$$LI_{ij} = u_{ij} - a_{ij}$$

$$MCA_{ij} = \frac{\dfrac{u_{ij}}{a_{ij}}}{\displaystyle\sum_{i=1}^{N_j}\dfrac{u_{ij}}{a_{ij}}}$$

Pelagic habitat was characterized by the selectivity curves using seasonal 0.1° latitude/longitude climatological fields as a predictive baseline. A high-resolution lookup table was created for each selectivity curve to enable prediction for each pixel of the grids. A multivariate habitat map was constructed using each of the LI selectivity curves as an additive component towards the final habitat preference index. Weighting of the component LI with weights W was explored. The meta type habitat index, H, was created from the standardized LI of the N_{KS} significant variables as follows:

$$H = \sum_{k=1}^{N_{KS}} LI_k \times W_k$$

Seasonal values of H were mapped across the entire North Pacific Basin. Suitable habitat was delineated by an arbitrary

threshold value determined from inspection of the overall H frequency distributions and locations of tracked individuals.

The performance of the multivariate habitat prediction was tested using more recently available raw satellite track data for loggerhead sea turtles in late 2006 and early 2007. Data subsequent to July 2006 were not included in the habitat characterization study and served as an ideal test of habitat utilization. Habitat index values were calculated for the test dataset of tracks after merging the five environmental variables to the newer data, and this distribution was compared to the original distribution using a two-sample Kolmogorov–Smirnov test. The distributions should be similar if the habitat characterization is robust.

3. Results

As of the time of this analysis in mid-2006, 186 tracks ranging in duration from 1.25 to 945.3 days have been recorded (Table 1), with total distance traveled ranging from 13.6 to 17,906.5 km

Table 2
Summary of modified Kolmogorov–Smirnov (KS) statistical tests comparing cumulative frequency distributions of utilization and availability of 16 environmental variables merged with pelagic loggerhead sea turtle satellite track data

Environmental variable	Kolmogorov–Smirnov D_{max} value	Value at D_{max}	Significance
SeaWiFS chlorophyll a	0.3596	0.1050	***
Pathfinder sea surface temperature	0.2985	19.8500	***
IGRF-10 magnetic declination	0.2669	12.1485	***
IGRF-10 magnetic total force	0.1998	44136.5	***
IGRF-10 magnetic inclination	0.1866	53.8970	**
AVISO geostrophic u-component	0.1516	4.5000	ns
Smith & Sandwell bathymetry	0.1486	−5485	ns
AVISO sea surface height	0.1476	171.5	ns
Pathfinder sea surface temperature gradient	0.1303	0.1350	ns
ERS/QuikSCAT winds u-component	0.1106	−0.0212	ns
IGRF-10 magnetic orthogonality index	0.1097	0.0786	ns
ERS/QuikSCAT winds v-component	0.1002	−0.0042	ns
AVISO geostrophic v-component	0.0707	−8.5	ns
ERS/QuikSCAT winds total magnitude	0.0665	0.1859	ns
Smith & Sandwell bathymetric EW gradient	0.0300	−315	ns
Smith & Sandwell bathymetric NS gradient	0.0133	−625	ns

Asterisks denote significance at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***) levels of probability, corresponding to Bonferroni adjusted critical values for D_{max} of 0.1535, 0.1717, and 0.1948, respectively. In a KS test, D_{max} represents the largest absolute vertical distance between any 2 horizontal locations on an overlaid cumulative frequency distribution plot. This value where D_{max} occurs is presented above.
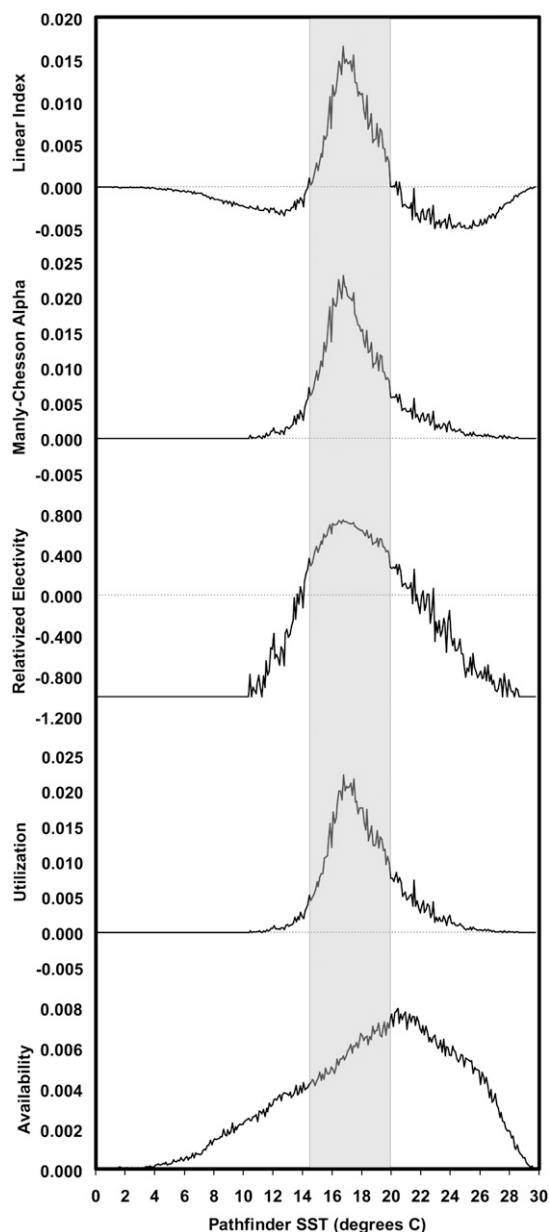
Fig. 4. Availability, utilization, and loggerhead sea turtle selection curves estimated for Pathfinder SST per 0.1 °C bins. Availability represents overall frequency distribution from 150°E–130°W longitude, 27°N–44°N latitude, January, 1997–December, 2006. Utilization represents overall frequency distribution from data merged to all pelagic satellite tracks. RE refers to the Relativized Electivity index, MCA refers to the Manly–Chesson–Alpha index, and LI refers to the Linear Index. Shaded region represents positive values of the LI (14.45 °C–19.95 °C) for reference.

(integrated along entire track). The average track spanned 257.9 days and covered 5648.9 km, for an average speed of 21.9 km per day. A broad size range of wild and captive-reared individuals were tagged and released, ranging from 25.6 to 89.1 cm SCL at locations across the North Pacific (Fig. 1). The mean size of tracked individuals was 48.3 cm SCL. Individuals did not simply radiate from a single point of release and there were strong indications of directed orientation that was qualitatively similar between years and size classes of individuals.

The NMDS analysis suggested that data ensembles to the easternmost and westernmost of the North Pacific Basin were exhibiting different characteristics with respect to latitudinal distributions (Fig. 3). Season of the year and turtle size did not correlate to any pattern in the resulting NMDS ordination scatterplot. Subsequent analyses were performed on the pelagic subset of satellite tags ($n=135$) between 150°E and 130°W longitude. There was no strong indication from the latitudinal analysis of further data groupings based on size, longitude or season; therefore, all pelagic track data was aggregated for this analysis of habitat.

The modified KS statistical tests indicated that 5 of the 16 environmental variables examined were significantly different in
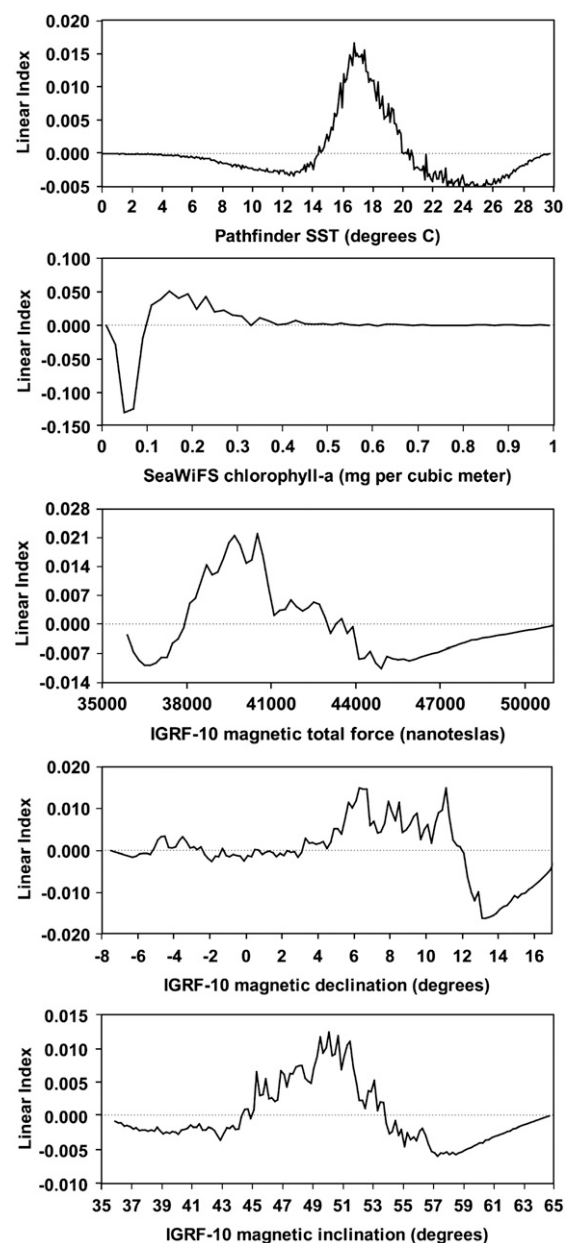

Fig. 5. Linear Index (LI) for the five statistically significant environmental variables from the modified Kolmogorov–Smirnov test. LIs are shown for Pathfinder SST, SeaWiFS chlorophyll *a*, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination.

Table 3
Environmental variable range of values for pelagic habitat definition of loggerhead sea turtles, based on criteria of positive Linear Index

Variable	Range definition for habitat
Pathfinder SST	14.45 °C to 19.95 °C
SeaWiFS chlorophyll a	0.11 mg/m^3 to 0.31 mg/m^3
IGRF-10 magnetic force	38,100 nT to 42,900 nT
IGRF-10 magnetic declination	−5.1° to −2.5°, 3.3° to 11.9°
IGRF-10 magnetic inclination	44.5° to 53.7°

utilization and availability. SeaWiFS chlorophyll a, Pathfinder SST, and 3 IGRF-10 magnetic field variables (total force, declination, and inclination) had strongly different cumulative frequency distributions. The largest D_{max} values occurred at 0.1050 mg chlorophyll a per cubic meter, 19.85 °C sea surface temperature, 44136.5 nT magnetic total force, 12.1485° magnetic declination, and 53.897° magnetic inclination (Table 2).

Example selectivity curves for Pathfinder SST are shown in Fig. 4. Note that RE and LI can vary in both positive and negative directions, indicative of preference and avoidance, respectively. MCA is always positive and is intended to measure biologically based preference over the range of resources sampled (Chesson, 1978, 1983). The utilization and availability distributions for SST are also shown as an example (Fig. 4). The simplicity and well-behaved nature of the LI index is appealing, as well as the intuitive logic of an index which can be negative for resources not preferred. The odd behavior of the RE index in the negative domain is not clearly understood, and it is also unclear why the region of preference is much broader than both LI and MCA would indicate; the raw utilization distribution is more consistent with the shapes of the LI and MCA curves
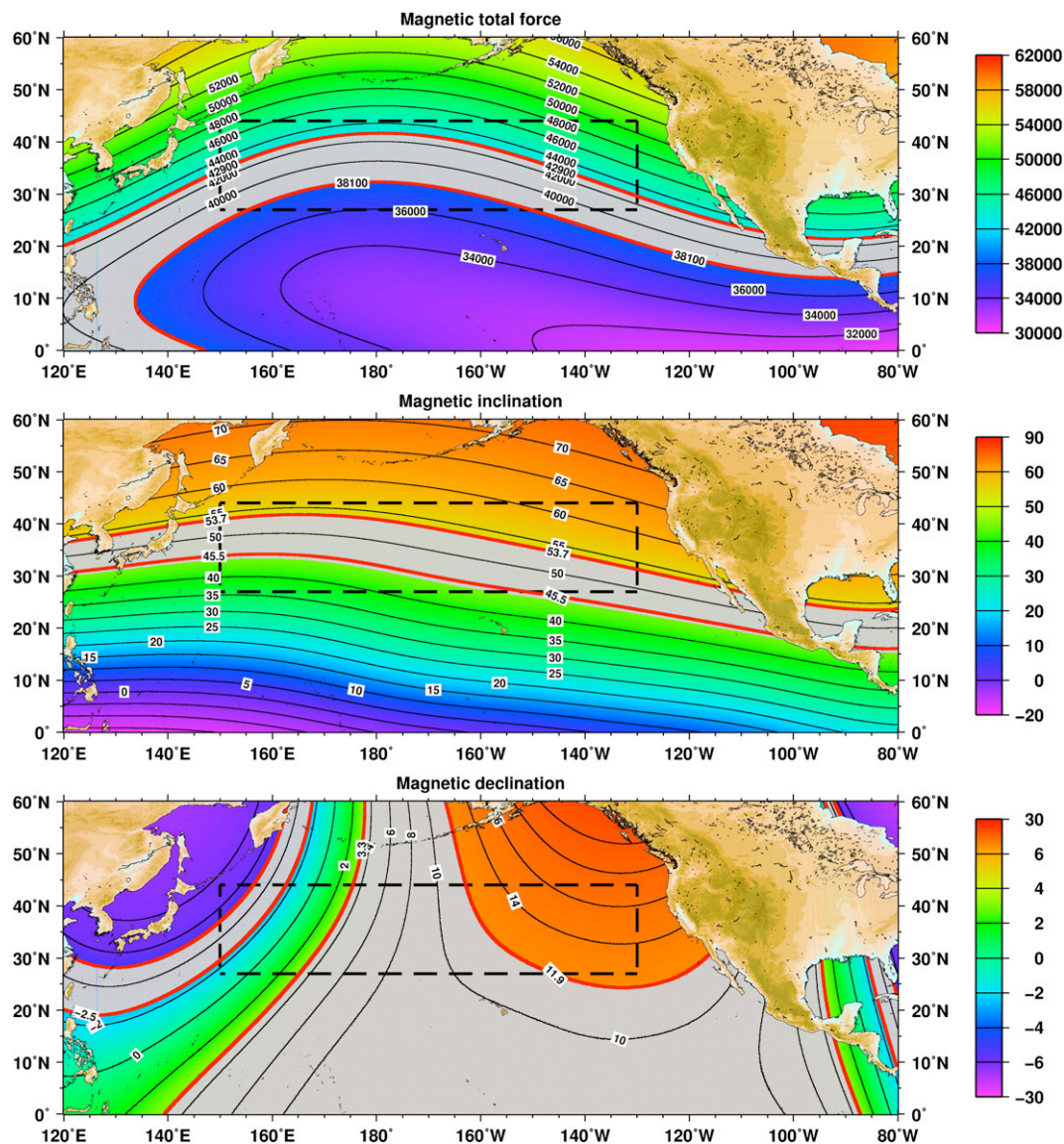

Fig. 6. Example IGRF-10 earth magnetic field grids (total force, inclination, and declination from top to bottom, respectively) from May 2007. Loggerhead sea turtle pelagic habitat ranges for each variable are outlined in red and stippled in gray. Dashed line delineates grid used for pelagic habitat study, 150°E–130°W longitude, 27°N–44°N latitude.

(Fig. 4). For these reasons, further analyses focused on the LI results. LI curves for SeaWiFS chlorophyll *a*, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination are shown in Fig. 5.

Positive values of LI were used to delineate habitat ranges for each of the five statistically significant variables. Loggerhead sea turtle pelagic habitat was therefore defined by Pathfinder SST values from 14.45 °C to 19.95 °C, SeaWiFS chlorophyll *a* values from 0.11 mg/m³ to 0.31 mg/m³, IGRF-10 magnetic force values from 38,100 nT to 42,900 nT, IGRF-10 magnetic declination values from −5.1° to −2.5° and 3.3° to 11.9°, and IGRF-10 magnetic inclination values from 44.5° to 53.7° (Table 3). Since the spatial pattern of magnetic field data is not familiar to the average reader, the habitat ranges and overall pattern for the three IGRF-10 magnetic variables are shown in Fig. 6 for an example month (May 2007). It should be

noted that the earth magnetic field data used in this study change very slowly over time; however, the differences over the time scale of this analysis are barely perceptible to the human eye when plotted as in Fig. 6.

The multivariate habitat index, *H*, is shown for seasonal climatological grids in Figs. 7–10. Four versions of habitat are shown, utilizing the LI differentially. In the first habitat map, the LI of all five environmental variables are simply summed in unweighted fashion (Fig. 7). In the second habitat map, only the LI of Pathfinder SST is used (Fig. 8). In the third habitat map, the LI of Pathfinder SST and SeaWiFS chlorophyll *a* are used (Fig. 9). In the fourth habitat map, the LI of all five environmental variables are summed in weighted fashion (Fig. 10). Various weighting factors were explored. Since utilization of three components of the earth magnetic field is likely redundant in the habitat index, an attempt was made to weight these component LI correspondingly

Fig. 7. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST, SeaWiFS chlorophyll *a*, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination. All five variables combined equally for the final habitat index.

Fig. 8. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Habitat index is derived from the LI selection curve for Pathfinder SST only.

less than SST and chlorophyll *a* LI. Temperature is likely linked to more fundamental metabolic or innate responses and received a higher weight than the component likely related to forage (chlorophyll *a*). A tentative weighting scheme of (1.0, 0.5, 0.1, 0.1, 0.1) is presented here for the calculation of *H* from component LI of SST, chlorophyll *a*, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination, respectively (Fig. 10).

Loggerhead sea turtle satellite track data in late 2006 and early 2007 primarily occurred within the delineated habitat predicted by the multivariate *H* index. The two-sample Kolmogorov–Smirnov test indicated that the cumulative frequency distribution of weighted *H* values from the original track data was not significantly different from the cumulative frequency distribution of the newer 2006–2007 track data not used in the habitat characterization ($D_{max}=0.1295$, $p>0.05$,

$N_1=135$, $N_2=66$, $D_{0.05}=0.2037$). The percent distributions of the weighted habitat index are shown in Fig. 11.

4. Discussion

Quantitative evaluation of habitat preference may be improved by analytical tools developed in the foraging field of study. Both of these processes are shared elements of the broader field of resource selection, and common approaches can apply (Manly et al., 2002). With the now widespread use of satellite tags and other data-intensive approaches, it will be very useful to apply methodologies that can distill the massive amounts of data into simplified and ecologically meaningful results. Resource selection indices should be further explored as a technique in satellite tag research, and may have broad applicability toward habitat-related issues such as mitigation of protected species
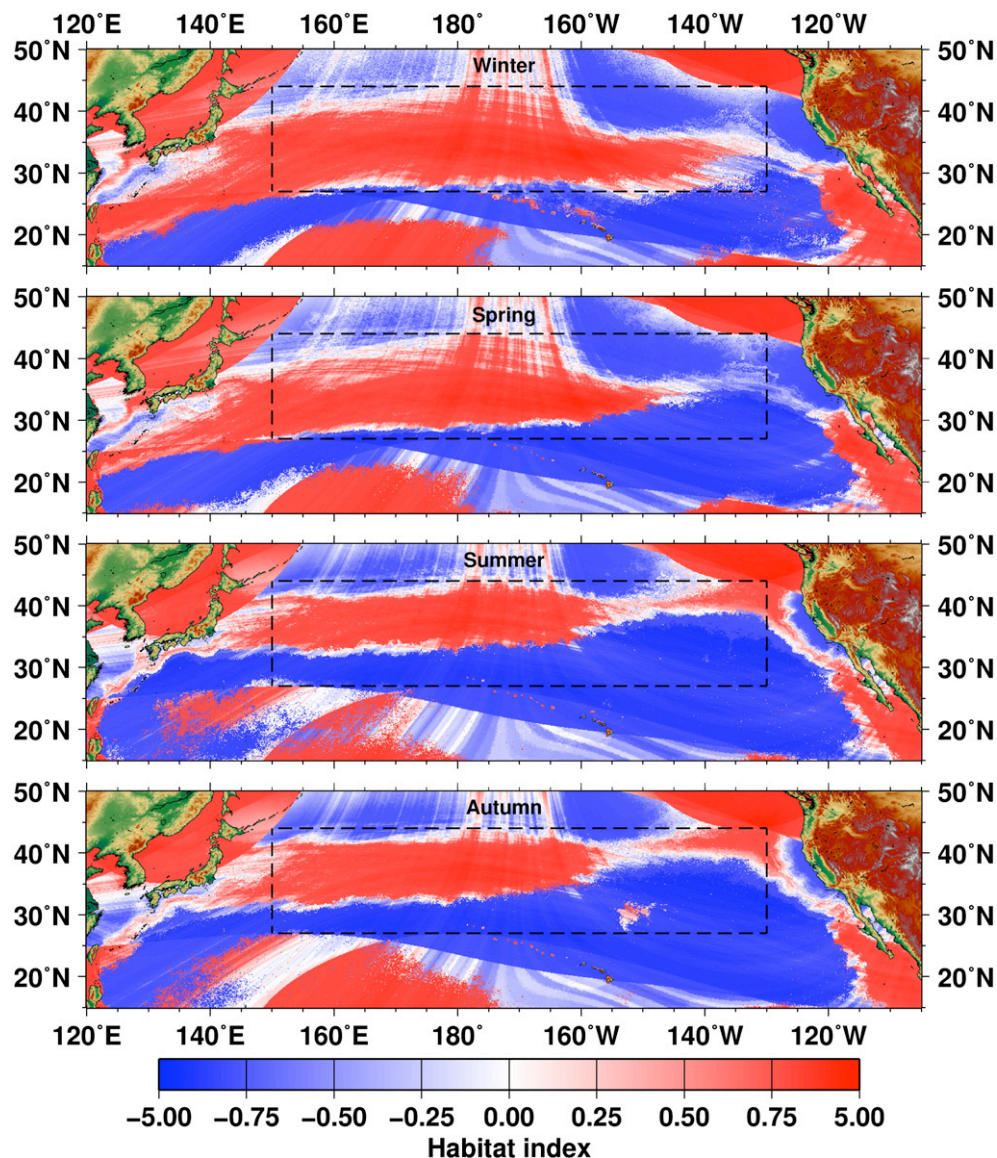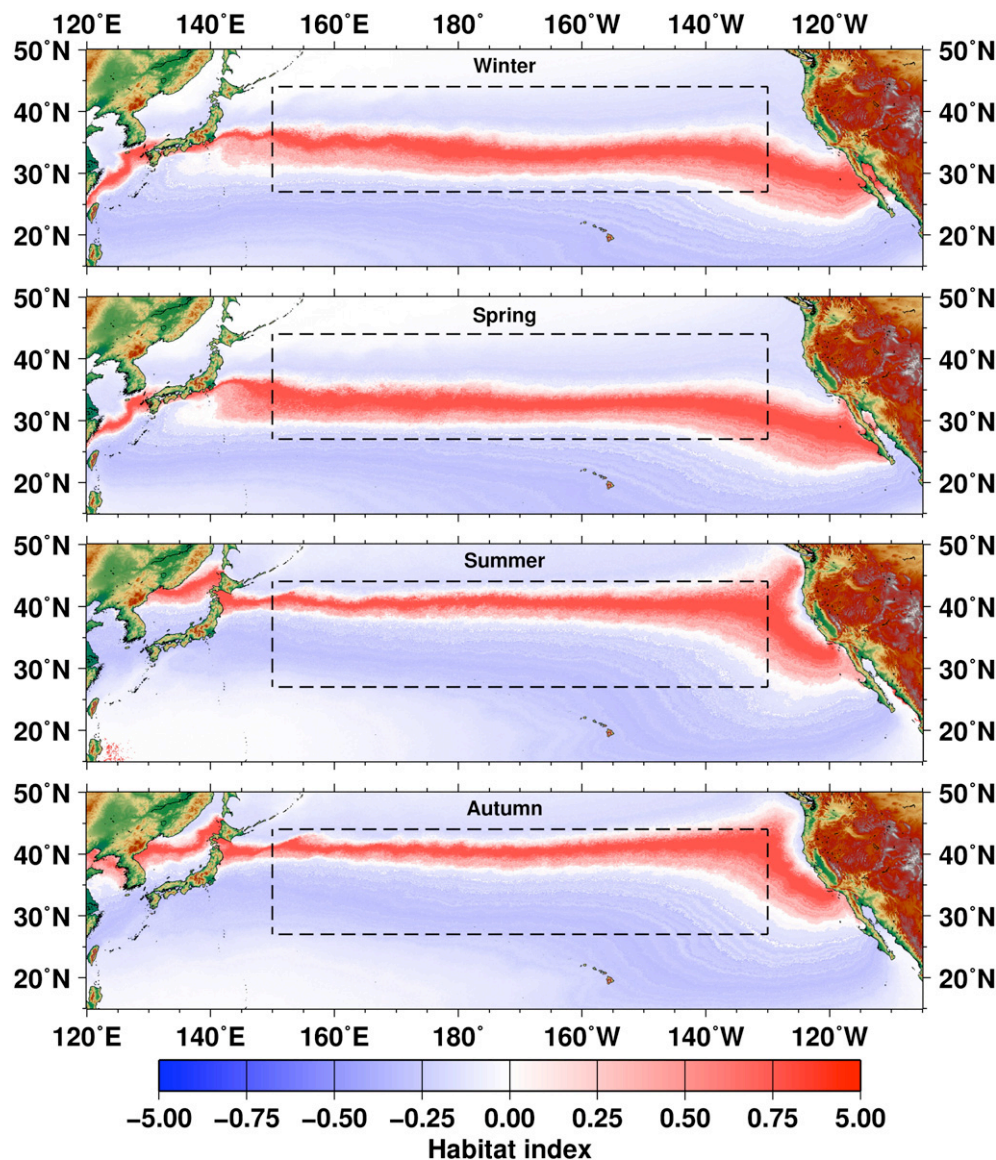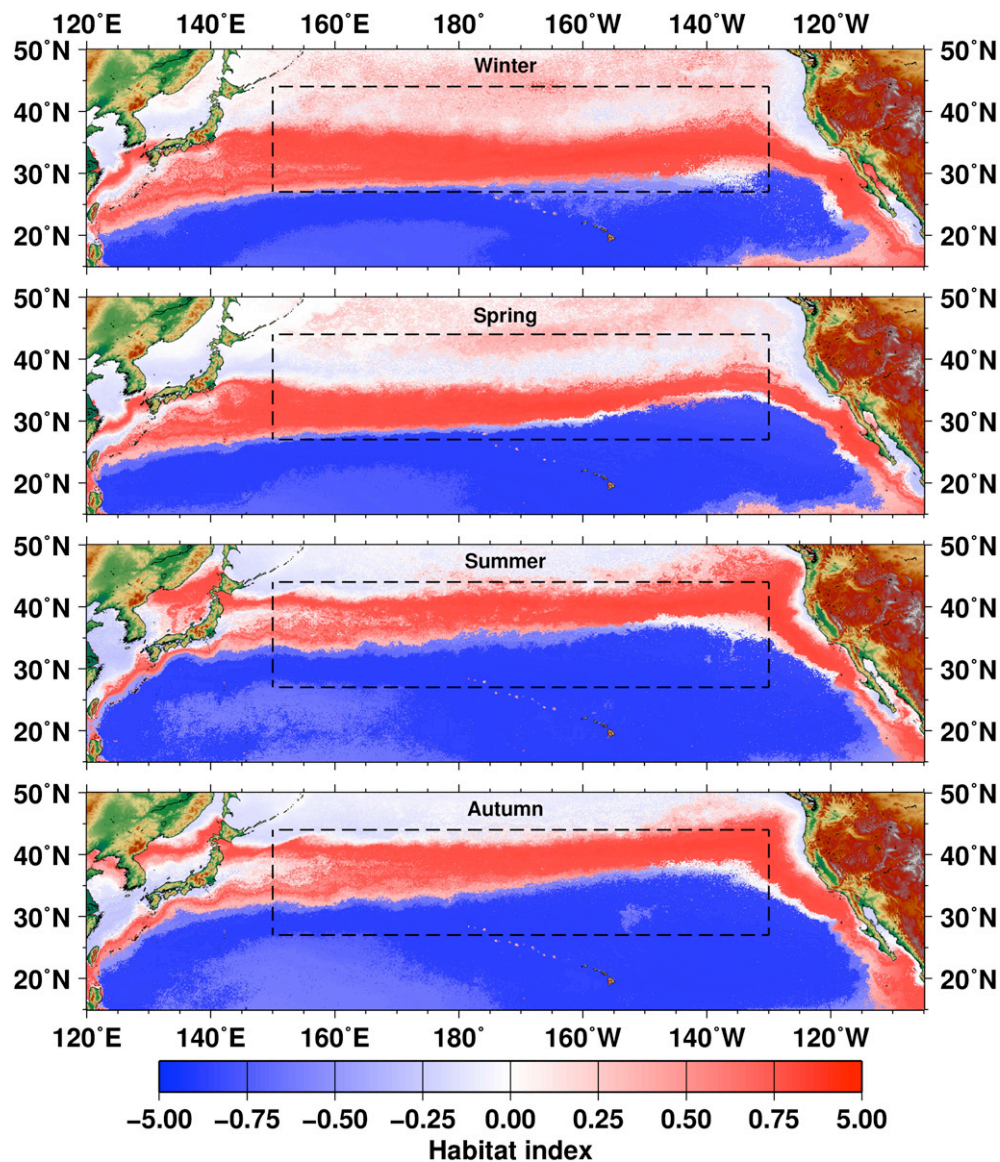
Fig. 9. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST and SeaWiFS chlorophyll *a*.

interactions with fisheries, Marine Protected Areas, Essential Fish Habitat, and ecosystem management. The quantification of habitat is a critical element of successful management of highly migratory species (Cañadas et al., 2005; Louzao et al., 2006). Some researchers have used Ivlev's Index of Electivity (Ivlev, 1961) to characterize habitat preference (Carreras et al., 2004; Cardona et al., 2005; Revelles et al., 2007a), despite this approach being considered deprecated for use in forage studies (Cock, 1978; Chesson, 1978; Lechowicz, 1982) because of statistical concerns. The implications of this are unclear, yet caution is warranted since resource utilization, whether forage or habitat, is a single process with much literature on relevant analytical tools and their performance or lack thereof. The Linear Index of Strauss (1979) is promoted here as a tool for habitat characterization since it offers a simple, objective means of determining preferred or non-preferred ranges for a particular

environmental variable, and the index is well-behaved over a finite negative to positive range of values.

The finding that SST and chlorophyll *a* characterize the loggerhead sea turtle pelagic habitat is consistent with earlier studies based on fewer turtles over a smaller temporal and spatial range (Polovina et al., 2000, 2004, 2006). In particular the preferred range of surface chlorophyll *a* habitat identified in this study (0.1–0.3 mg/m^3) is interpreted as identifying the Transition Zone Chlorophyll Front (TZCF) as an important loggerhead sea turtle foraging habitat. The TZCF is a basin-wide surface chlorophyll *a* front that represents the boundary between the warm, vertically stratified, low surface chlorophyll *a* water of the subtropical gyre and the vertically mixed cool, higher surface chlorophyll *a* Transition Zone water (Polovina et al., 2001). The TZCF is defined to be located at surface chlorophyll *a* level of 0.2 mg/m^3 and thought to represent a
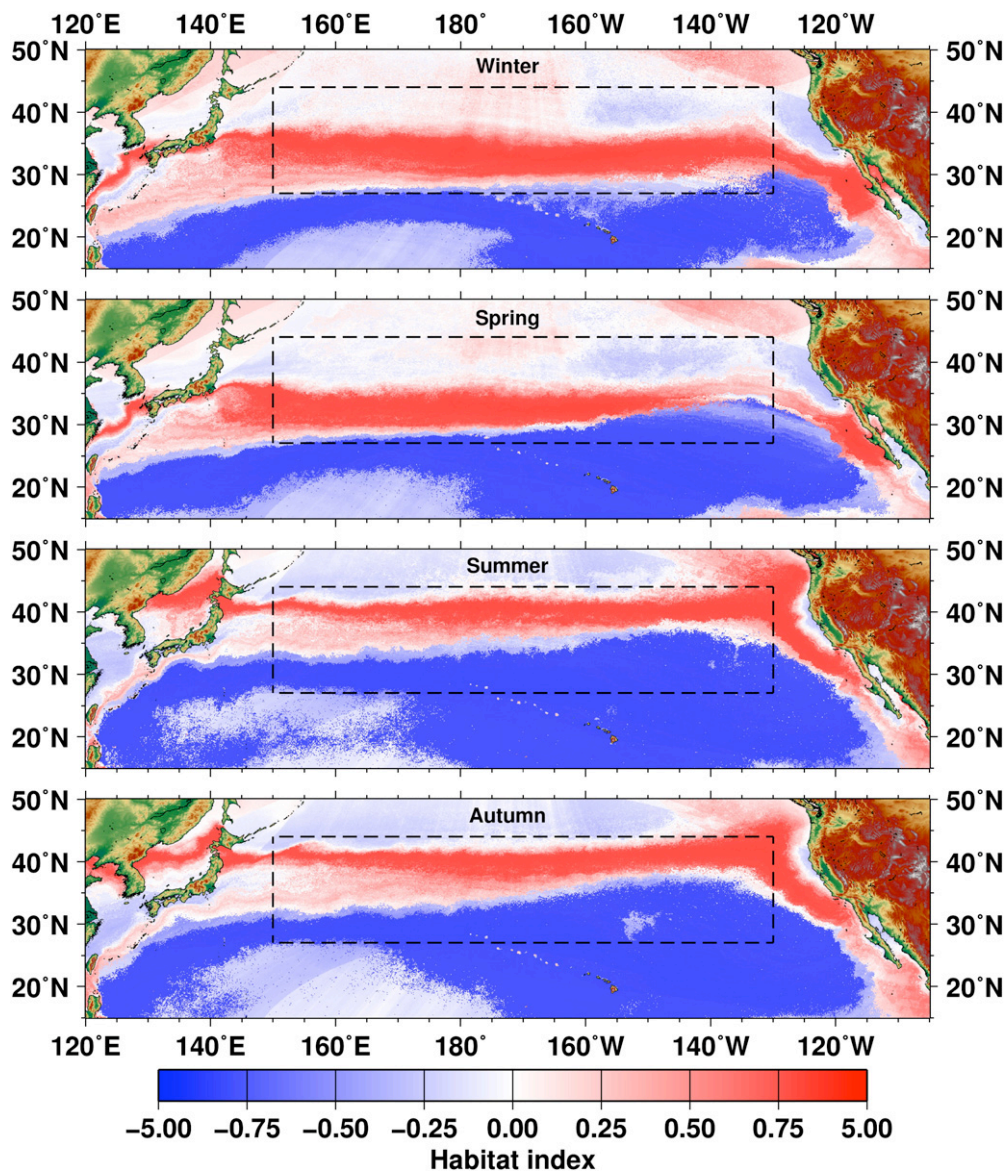
Fig. 10. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST, SeaWiFS chlorophyll *a*, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination. Five variables combined with weights of 1.0, 0.5, 0.1, 0.1, and 0.1, respectively for the final habitat index.

zone of surface convergence that would concentrate the buoyant, surface prey of loggerheads (Polovina et al., 2001; Parker et al., 2005). Forage issues have been shown to be a strong determinant of habitat selection in other pelagic animals such as leatherback sea turtles (Houghton et al., 2006) and sea lions (Fowler et al., 2006). Pathfinder SST and SeaWiFS chlorophyll *a* are possible proxies to forage availability and abundance; furthermore, these two candidate variables display the most temporal and spatial variability, relative to the IGRF-10 variables, and correlate well to the seasonal and interannual patterns observed in the data. For example, when summarized against latitude for individual years, the satellite tracks appear to correspond closely to interannual and seasonal variability in SST (Fig. 12) and chlorophyll *a* (Fig. 13). Forage fields in the North Pacific are not as well known as in the North Atlantic (Hays, 1996), yet relevant ecosystem level approaches are

beginning to clarify the relationships between physical oceanography, productivity, and forage availability for higher trophic level organisms in the North Pacific pelagic environment (e.g., Batten et al., 2006).

Many aspects of life history often reflect evolutionary adaptations or trade-offs in 3 important areas: foraging/growth, reproduction, and avoiding predators. It follows that habitat selection can be related to one or all of the above. Reproduction is not likely a factor in loggerhead pelagic habitat since mating and nesting occur in coastal areas. It remains possible that loggerhead habitat selection is related to predator avoidance, since this has been found to be important in certain green sea turtle (*Chelonia mydas*) habitat studies (Heithaus et al., 2007, 2008-this issue). Clearly, more work is needed on the predator/prey dynamics of pelagic loggerhead sea turtles, from both perspectives. It should be noted, however, that tiger sharks and
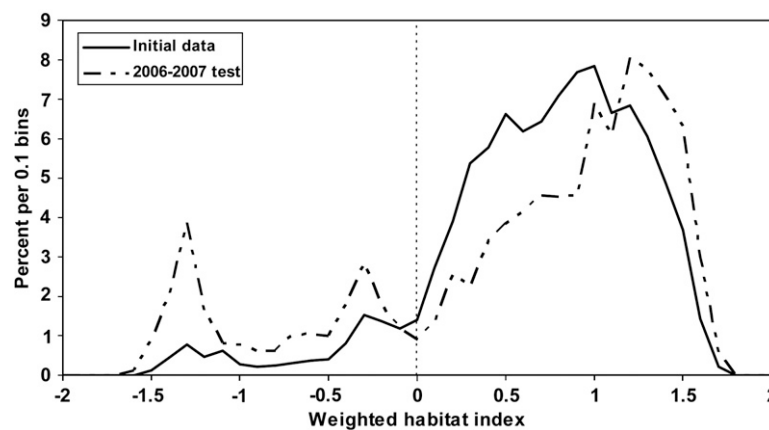
Fig. 11. Percent distributions of the weighted habitat index for the initial data used in this study (solid line) and the 2006–2007 test data (dashed line). A two-sample Kolmogorov–Smirnov test indicated that the distributions were not significantly different ($D_{max}=0.1295$, $p>0.05$, $N_1=135$, $N_2=66$, $D_{0.05}=0.2037$). The vertical dotted line separates presumed avoidance from preference.

great white sharks, 2 likely predators in this general region, are not known to be foraging heavily in the pelagic North Pacific (Holland et al., 1999; Weng et al., 2007). It remains likely that foraging issues are the primary determinant of loggerhead pelagic habitat selection in this portion of their life history.

The importance of SST implies that preferred habitat may be seriously impinged on by trends in ocean temperature, for example El Niño Southern Oscillation events, climate change, or global warming may reposition migratory pathways, and possibly remap critical intersections with high-seas fisheries. The issue of bycatch mitigation is extremely important, as the incidental take of sea turtles has closed or severely restricted fishing activities where interactions occur. The pelagic habitat maps presented here may be useful for reducing interactions with high-seas fisheries, in conjunction with real-time products such as the PIFSC TurtleWatch Program (http://www.pifsc. noaa.gov/eod/turtlewatch.php).

In addition to the two oceanographic variables, three magnetic variables also emerged as potentially defining loggerhead habitat. This is the first treatment of loggerhead habitat in the Pacific that brings into consideration the potential importance of magnetic variables. Laboratory studies performed upon Atlantic loggerhead sea turtle hatchlings have shown that magnetic total force and magnetic inclination are detectable (Light et al., 1993; Lohmann and Lohmann, 1996). Detection of magnetic declination *per se* has not been documented in this species, yet the plausibility of determining declination is discussed by Lohmann and Lohmann (2006). Organisms which have the ability to detect true-north, via stellar navigation for example, could easily determine magnetic declination by comparing the
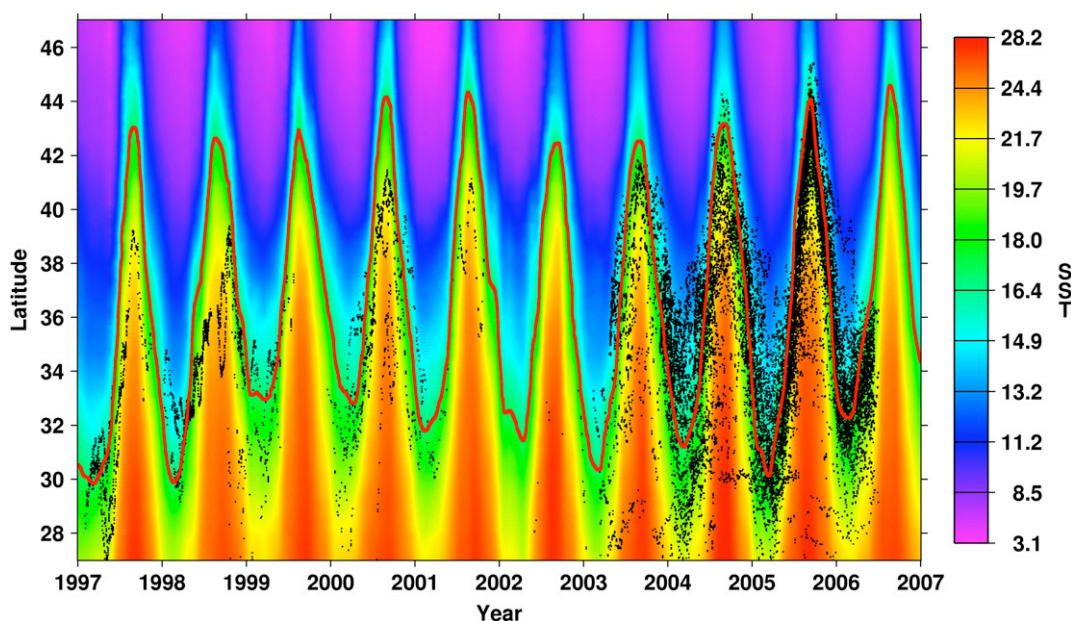

Fig. 12. Mean Pathfinder SST (°C) by latitude (*y*-axis) and time (*x*-axis). All loggerhead sea turtle satellite track data are also shown (black dots) for the corresponding latitude and time of the satellite fix (spanning January 1997–July 2006). Mean SST is from 180°–160°W longitude, thick red line is the 17° isotherm for reference.
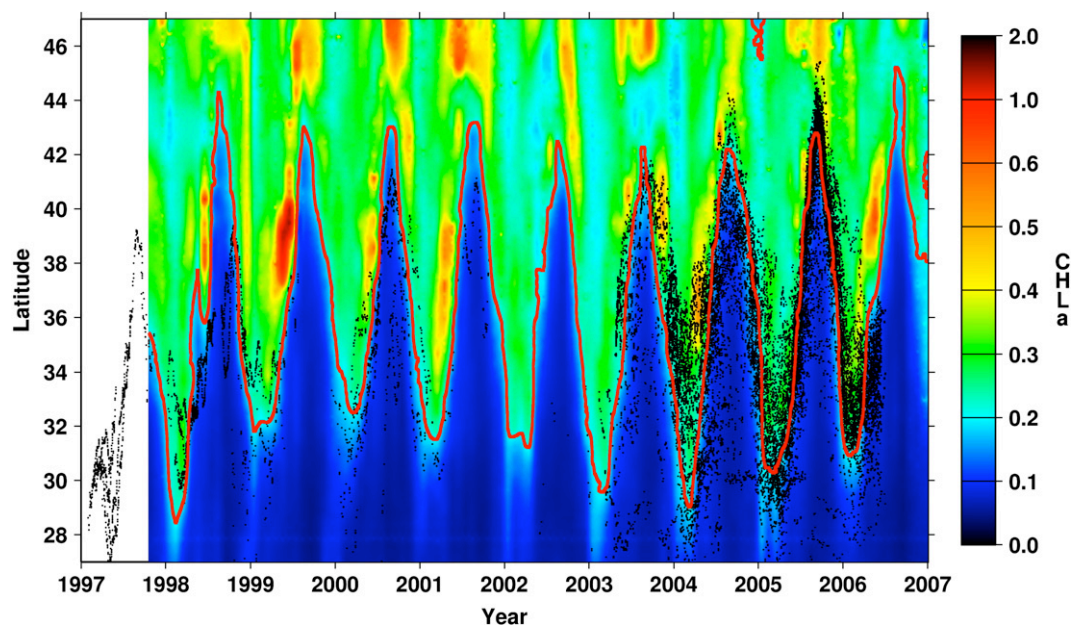
Fig. 13. Mean SeaWiFS chlorophyll *a* concentration (mg/m^3) by latitude (*y*-axis) and time (*x*-axis). All loggerhead sea turtle satellite track data are also shown (black dots) for the corresponding latitude and time of the satellite fix (spanning January 1997–July 2006). Mean chlorophyll *a* is from 180°–160°W longitude, thick red line is the 0.2 mg/m^3 isoline for reference. SeaWiFS data is available from September 1997 onward.

true-north information with a magnetic compass. Such magnetic compasses have been found to be very widespread throughout the animal kingdom, including sea turtles (Wiltschko and Wiltschko, 1995). Pelagic orientation in the North Pacific Ocean may be the closest example of "swimming the isoline" hypothesis of Lohmann and Lohmann (2006), who suggested the possibility of sea turtles simply swimming along some constant value in the earth magnetic field. For example, the apparent curvature of loggerhead tracks in mid-basin in the North Pacific Ocean (Fig. 1) may correspond to individuals following isolines or contours (lines of constant value) of magnetic total force or magnetic inclination, both of which have slightly domed shapes (Fig. 6). Individuals following either the ~40,000 nT magnetic total force contour or the ~50° magnetic inclination contour could maintain relative proximity to the observed migratory pathway. These values are markedly different from values that would be practical for loggerhead sea turtles in the Atlantic. Likewise, there are many differences in oceanography between the two basins, and localized adaptation or individual learning is therefore likely since this species is found to be genetically heterogeneous over its range (Bowen et al., 1994). While magnetic fields are clearly used by some sea turtles, experimental evidence suggests that other navigational aids must also be important (Luschi et al., 2007). The parameterization of loggerhead pelagic habitat with several environmental variables as conducted in this analysis is clearly supported by scientific findings to date. Future studies need to carefully quantify the navigational mechanisms used at different portions of the life history, since hatchlings have different behavioral and ecological needs than older stages.

The futility of an organism using any single environmental variable for habitat orientation is best seen with IGRF-10 magnetic declination. While this variable was statistically significant,

individually it is very unlikely to explain the observed distributional pattern of loggerhead sea turtles (Fig. 6, lower panel), since the habitat bounds extend zonally into regions of the Pacific Ocean regions where loggerhead sea turtles do not occur (Dodd, 1988; Eckert, 1993). While exact orientation cues used in real-time by pelagic loggerhead sea turtles remain unknown, it would seem likely and evolutionarily advantageous to have more than a single navigational aid. It is plausible that certain variables serve as a general guide, locating the organism crudely in preferred regions, coupled with variables which are more detailed spatially, for fine-tuning of position. Magnetic fields could be the general cue, with oceanography serving as the specific cue. Such polyphasic navigational models have been proposed by Bingman and Cheng (2005), whereby different models of navigation are used by an organism depending on immediate data availability and its ecological needs. The concept of bi-coordinate magnetic maps (Lohmann and Lohmann, 2006) was explored here with the IGRF-10 index of orthogonality (between total force and inclination), but this variable was not found to correspond to habitat utilization. Considering the similarity of magnetic total force and inclination fields in the North Pacific (Fig. 6), a bi-coordinate system that uses magnetic declination and either magnetic total force or magnetic inclination would perform nearly as well as a Cartesian coordinate system such as latitude and longitude. Clearly, more work in this area is needed, both descriptive and experimental.

The sea surface height and related variables were not found to be significant in characterizing pelagic habitat. These features are not deemed unimportant, only not amenable to being a habitat descriptor. Geostrophic features are known to be very important towards foraging habitat (Polovina et al., 2006). Bathymetric variables were also unuseful descriptors of pelagic habitat, although as mentioned below may be more useful when examining the coastal behavior and habitat characterization. Wind

is potentially a very important variable locally, but like sea surface height, does not seem to be a likely habitat cue basin-wide.

The final weighting scheme for the pelagic habitat characterization is tentatively proposed to effectively merge the five environmental variables in a meaningful way. The magnetic information brings interesting new patterns to the predicted habitat, e.g., the mid-basin deformation may be critical towards separating purely latitudinal or SST patterns from the influence of other habitat variables. Interestingly, bifurcations in habitat appear when SeaWiFS chlorophyll *a* is included in the habitat, as well as significant habitat range extensions. Such bifurcations, broadening/narrowing, and gradients of the habitat index offer much in the way of hypothesis-testing for future work.

Tagging data analyzed by other researchers have suggested that sea turtle pelagic movement can be significantly passive (Luschi et al., 2003, Revelles et al., 2007b). However, even post-hatching loggerheads have well-developed swimming skills (O'Hara, 1980; Davenport and Clough, 1986) and have been characterized as "smart" drifters (Witherington, 2002) with alternating periods of passive floating and directed swimming based on suitability of forage and habitat. A similar finding for biphasic behavior was found in Mediterranean adult loggerhead sea turtles (Bentivegna et al., 2007). Subadult and juvenile loggerhead sea turtles in the North Pacific are thought to be actively swimming most of the time (Polovina et al., 2000, 2004). Satellite track analysis should incorporate ocean currents to better understand movement dynamics (Gaspar et al., 2006), and the tag unit itself would benefit from nonmagnetic-interference means of determining the orientation of the sea turtle, i.e., what direction is the sea turtle facing, and also how much swimming effort is being expended (e.g., flipper beats). Hays et al. (2004) used a small sensor for measuring and storing green sea turtle flipper beats during diving behavior; unfortunately, this device involves powerful rare-earth magnets (Wilson and Liebsch, 2003) which could potentially interfere with magnetic navigation. Crittercam has also proven useful for measuring sea turtle flipper beat frequency (Hays et al., 2007) and, coupled with a simple compass in view of the camera, could provide the necessary data although this approach requires very time-consuming extraction of data via frame-by-frame visual inspection. Ideally, a small electronic package would record, summarize, and compress the pertinent data into a format that could then be transmitted in the Argos satellite data stream as described by Myers et al. (2006). Specialized bio-loggers have proven to be very useful for understanding swimming behavior in other taxa such as finfish (e.g., Kawabe et al., 2004) and birds (e.g., Ropert-Coudert et al., 2006). In comparison to these taxa, sea turtles are an optimal platform for this type of work (size, carapace for attachment points, epipelagic habitat, and behavior), which will allow a better understanding of the relationship between swimming behavior and background current fields.

Our future work on loggerhead sea turtle pelagic habitat will evaluate the role of ocean currents on the distribution and abundance of pelagic loggerhead sea turtles, as well as the role of other variables not examined in this study, such as ocean current convergence, wind stress curl, and ocean productivity. Further work with the *H* index, and how to effectively apply

diverse LI simultaneously is also needed. The presently used availability measure covers a large time and space domain of values; undoubtedly, this is a crude measure and, as more behavior is incorporated into the habitat selection process, the availability measure should be refined accordingly. The track randomization approach of Heithaus et al. (2002, 2006) offers much promise towards characterization of microhabitat using tracking information. This effort should also coincide with further analyses on the spatial autocorrelation in the environmental data grids, possibly with variogram approaches to quantify this (e.g., Liebhold and Sharov, 1998). The subsurface aspect of pelagic habitat will also be investigated, since pelagic diving behavior is common (Polovina et al., 2003), and diving behavior can be a critical component of habitat selection behavior in pelagic organisms (e.g., Sims et al., 2005; Sale et al., 2006). Application of an ecosystem approach which takes into account the vertical distribution of forage will be important in this regard (e.g., Batten et al., 2006). Coastal behavior of loggerhead sea turtles will also be quantified in a subsequent study. Pelagic foraging behavior off the coastline of Baja California Sur appears to be a specialized pattern related to high concentrations of pelagic red crabs, *Pleuroncodes planipes*, and is not a subset of normal pelagic behavior (Peckham and Nichols, 2003; Etnoyer et al., 2006). Coastal behavior in the Western Pacific may be primarily related to nesting and dispersal from nesting areas (Kamezaki et al., 2003; Cheng and Chen, 1997) and may require a more focused, regional study such as that done by Schofield et al. (2007). Bathymetry, proximity to shore, shoreline type, and forage availability may be more important coastal habitat variables.

5. Conclusion

Satellite track data for 186 loggerhead sea turtles in the North Pacific Ocean were merged to remotely sensed environmental data in an analysis to characterize pelagic habitat. Five statistically significant variables were identified out of the sixteen environmental variables examined using a modified KS test. Two of the oceanographic variables have strong seasonal, interannual, and spatial patterns (sea surface temperature and chlorophyll *a* concentration), while three others were strongly spatial and relatively static (earth magnetic force, earth magnetic declination, and earth magnetic inclination). Habitat selectivity for these variables was quantified using the Linear Index preference curve methodology established in the foraging literature. The output from the selectivity curves was used to predict a multivariate loggerhead sea turtle habitat index across the pelagic North Pacific.

References

Alfaro-Shigueto, J., Dutton, P.H., Mangel, J., Vega, D., 2004. First confirmed occurrence of loggerhead turtles in Peru. Marine Turtle Newsletter 103, 7–11.

Balazs, G.H., Miya, R.K., Beavers, S.C., 1996. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath, J.A., Barnard, D.E., Musick, J.A., Bell, B.A. (Eds.), Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. United States Department of Commerce, pp. 21–26.

Batten, S.D., Hyrenbach, K.D., Sydeman, W.J., Henry, M., Morgan, K.H., Welch, D., 2006. Characterizing meso-marine ecosystems of the North Pacific. Deep-Sea Research II 53, 270–290.

Bentivegna, F., Valentino, F., Falco, P., Zambianchi, E., Hochscheid, S., 2007. The relationship between loggerhead turtle (*Caretta caretta*) movement patterns and Mediterranean currents. Marine Biology 151, 1605–1614.

Bingman, V.P., Cheng, K., 2005. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. Ethology Ecology and Evolution 17, 295–318.

Bolten, A.B., Bjorndal, K.A., Martins, H.R., Dellinger, T., Biscoito, M.J., Encalada, S.E., Bowen, B.W., 1998. Trans-Atlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analyses. Ecological Applications 8, 1–7.

Bowen, B.W., Kamezaki, N., Limpus, C.J., Hughes, G.R., Meylan, A.B., Avise, J.C., 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. Evolution 48, 1820–1828.

Bowen, B.W., Abreu-Grobois, F.A., Balazs, G.H., Kamezaki, N., Limpus, C.J., Ferl, R.J., 1995. Trans-Pacific migrations of the loggerhead sea turtle demonstrated with mitochondrial DNA markers. Proceedings of the National Academy of Science, USA 92, 3731–3734.

Brodeur, R.D., 1998. Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. Environmental Biology of Fishes 51, 175–186.

Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., Hammond, P.S., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conservation: Marine and Freshwater Ecosystems 15, 495–521.

Cardona, L., Revelles, M., Carreras, C., San Félix, M., Gazo, M., Aguilar, A., 2005. Western Mediterranean immature loggerhead turtles: habitat use in spring and summer assessed through satellite tracking and aerial surveys. Marine Biology 147, 583–591.

Carr, A., 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1, 103–121.

Carreras, C., Cardona, L., Aguilar, A., 2004. Incidental catch of the loggerhead turtle *Caretta caretta* off the Balearic Islands (Western Mediterranean). Biological Conservation 117, 321–329.

Cheng, I.-J., Chen, T.H., 1997. The incidental capture of five species of sea turtles by coastal setnet fisheries in the eastern waters of Taiwan. Biological Conservation 82, 235–239.

Chesson, J., 1978. Measuring preference in selective predation. Ecology 59, 211–215.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Clifford, P., Richardson, S., Hemon, D., 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45, 123–134.

Cock, M.J.W., 1978. The assessment of preference. Journal of Animal Ecology 47, 805–816.

Confer, M.V., Moore, M.V., 1987. Interpreting selectivity indices calculated from field data or conditions of prey replacement. Canadian Journal of Fisheries and Aquatic Sciences 44, 1529–1533.

Davenport, J., Clough, W., 1986. Swimming and diving in young loggerhead sea turtles (*Caretta caretta* L.). Copeia 1986, 53–57.

Dodd, C.K.J., 1988. Synopsis of the Biological Data on the Loggerhead Sea Turtle *Caretta caretta* (Linnaeus 1758). United States Department of the Interior, Fish and Wildlife Service. 110 pp.

Eckert, K.L., 1993. The biology and population status of marine turtles in the North Pacific Ocean. United States Department of Commerce. 158 pp.

Ellis, D.M., Balazs, G.H., 1998. The use of the generic mapping tools program to plot ARGOS tracking data. In: Epperly, S.P., Braun, J. (Eds.), Proceedings of the Seventeenth Annual Sea Turtle Symposium, March 4–8, 1997, Orlando, Florida. United States Department of Commererce, pp. 166–168.

Etnoyer, P., Canny, D., Mate, B.R., Morgan, L.E., Ortega-Ortiz, J.G., Nichols, W.J., 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. Deep-Sea Research II 53, 340–358.

Fowler, S.L., Costa, D.P., Arnould, J.P., Gales, N.J., Kuhn, C.E., 2006. Ontogeny of diving behaviour in the Australian sea lion: trials of adolescence in a late bloomer. Journal of Animal Ecology 75, 358–367.

Gaspar, P., Georges, J.-Y., Lenoble, A., Ferraroli, S., Fossette, S., Le Maho, Y., 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track (07/11/2006). Proceedings of the Royal Society B: Biological Sciences 273, 2697–2702.

Govoni, J.J., Ortner, P.B., Al-Yamani, F., Hill, L.C., 1986. Selective feeding of spot, *Leiostomus xanthurus* and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. Marine Ecology Progress Series 28, 175–183.

Hays, G.C., 1996. Large scale patterns of diel vertical migration in the North Atlantic region. Deep-Sea Research 43, 1601–1615.

Hays, G.C., Metcalfe, J.D., Walne, A.W., Wilson, R.P., 2004. First records of flipper beat frequency during sea turtle diving. Journal of Experimental Marine Biology and Ecology 303, 243–260.

Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. Ecology 87, 2647–2656.

Hays, G.C., Marshall, G.J., Seminoff, J.A., 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. Marine Biology 150, 1003–1009.

Heithaus, M.R., Dill, L.M., Marshall, G.J., Buhleier, B., 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology 140, 237–248.

Heithaus, M.R., Hamilton, I.M., Wirsing, A.J., Dill, L.M., 2006. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. Journal of Animal Ecology 75, 666–676.

Heithaus, M.R., Fird, A., Wirsing, A.J., Dill, L.M., Fourqurean, J., Burkholder, D., Thomson, J., Bejder, L., 2007. State-dependent risk-taking by green sea turtles mediates top–down effects of tiger shark intimidation in a marine ecosystem. Journal of Animal Ecology 76, 837–844.

Heithaus, M.R., Wirsing, A.J., Thomson, J.A., Burkholder, D.A., 2008. A review of lethal and non-lethal effects of predators on adult marine turtles. Journal of Experimental Marine Biology and Ecology 356, 43–51 (this issue).

Holland, K.N., Wetherbee, B.M., Lowe, C.G., Meyer, C.G., 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Marine Biology 134, 665–673.

Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., Hays, G.C., 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87, 1967–1972.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187–211.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding of Fishes. New Haven, CT, USA, Yale University Press.

Jacobs, J., 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14, 413–417.

Kamezaki, N., Matsuzawa, K., Abe, O., Asakawa, H., Fukii, T., Goto, K., 2003. Loggerhead turtles nesting in Japan. In: Bolten, A., Witherington, B. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, DC, USA, pp. 210–217.

Kawabe, R., Naito, Y., Sato, K., Miyashita, K., Yamashita, N., 2004. Direct measurement of the swimming speed, tailbeat, and body angle of Japanese flounder (*Paralichthys olivaceus*). ICES Journal of Marine Science 61, 1080–1087.

Kinzie, R.A., 1988. Habitat utilization by Hawaiian stream fishes with reference to community structure in oceanic island streams. Environmental Biology of Fishes 22, 179–192.

Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. Oecologia 52, 22–30.

León, Y.M., Bjorndal, K.A., 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Marine Ecology Progress Series 245, 249–258.

Liebhold, A.M., Sharov, A.A., 1998. Testing for correlation in the presence of spatial autocorrelation in insect count data. In: Baumgartner, J., Brandmayr, P., Manley, B.F.J. (Eds.), Proceedings of the Ecology and Population Dynamics Section of the 20th International Congress of Entomology. Population and Community Ecology for Insect Management and Conservation. Balkema Publishers, Rotterdam, Netherlands, pp. 111–117.

Light, P., Salmon, M., Lohmann, K.J., 1993. Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. Journal of Experimental Biology 182, 1–10.

Lohmann, K.J., Lohmann, C.M.F., 1996. Detection of magnetic field intensity by sea turtles. Nature 380, 59–61.

Lohmann, K.J., Lohmann, C.M.F., 2006. Sea turtles, lobsters, and oceanic magnetic maps. Marine and Freshwater Behaviour and Physiology 39, 49–64.

Longhurst, A., 2006. Ecological Geography of the Sea. Academic Press, San Diego, CA, USA. 575 pp.

Louzao, M., Hyrenbach, K.D., Arcos, J.M., Abello, P., Gil Desola, L., Oro, D., 2006. Oceanographic habitat of a critically endangered Mediterranean Procellariiform: Implications for the design of marine protected areas. Ecological Applications 16, 1683–1695.

Lukoschek, V., McCormick, M.I., 2001. Ontogeny of diet shifts in a tropical benthic carnivorous fish, *Parupeneus barberinus* (Mullidae): relationship between foraging behaviour, habitat use, jaw size and prey selection. Marine Biology 138, 1099–1113.

Luschi, P., Hays, G.C., Papi, F., 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103, 293–302.

Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J., Benvenuti, S., 2007. Marine turtles use geomagnetic cues during open-sea homing. Current Biology 17, 126–133.

Manly, B.F.J., Miller, P., Cook, L.M., 1972. Analysis of a selective predation experiment. The American Naturalist 106, 719–736.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Boston, MA, USA.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MJM Press, Gleneden Beach, OR, USA.

McMahon, C.R., Hays, G.C., 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. Global Change Biology 12, 1330–1338.

Morrissey, J.F., Gruber, S.H., 1993. Habitat selection by juvenile lemon sharks, *Negaprion brevirostris*. Environmental Biology of Fishes 38, 311–319.

Myers, A.E., Lovell, P., Hays, G.C., 2006. Tools for studying animal behaviour: validation of dive profiles relayed via the Argos satellite system. Animal Behaviour 71, 989–993.

O'Hara, J., 1980. Thermal influences on the swimming speed of loggerhead turtle hatchlings. Copeia 1980, 773–780.

Pacheco, M.A.W., Henderson, A., 1996. Testing association between species abundance and a continuous variable with Kolmogorov–Smirnov statistics. Plant Ecology 124, 95–99.

Parker, D.M., Cooke, W.J., Balazs, G.H., 2005. Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. Fishery Bulletin 103, 142–152.

Peckham, H., Nichols, W.J., 2003. Why did the turtle cross the ocean? Pelagic red crabs and loggerhead turtles along the Baja California coast. In: Seminoff, J.A. (Ed.), Proceedings of the Twenty-second Annual Symposium on Sea Turtle Biology and Conservation, pp. 47–48.

Polovina, J.J., Kleiber, P., Kobayashi, D.R., 1999. Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996. Fishery Bulletin 97, 132–143.

Polovina, J.J., Kobayashi, D.R., Ellis, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts in the central North Pacific, 1997–1998. Fisheries Oceanography 9, 71–82.

Polovina, J.J., Howell, E.A., Kobayashi, D.R., Seki, M.P., 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. Progress in Oceanography 49, 469–483.

Polovina, J.J., Howell, E.A., Parker, D.M., Balazs, G.H., 2003. Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: might deep longline sets catch fewer turtles? Fishery Bulletin 101, 189–193.

Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fisheries Oceanography 13, 36–51.

Polovina, J.J., Uchida, I., Balazs, G.H., Howell, E.A., Parker, D.M., Dutton, P.H., 2006. The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. Deep-Sea Research II 53, 326–339.

Pyper, B.J., Peterman, R.M., 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences 55, 2127–2140.

Qiu, B., Chen, S., 2005. Variability of the Kuroshio Extension jet, recirculation gyre and mesoscale eddies on decadal timescales. Journal of Physical Oceanography 35, 2090–2103.

Revelles, M., Cardona, L., Aguilar, A., San Félix, M., Fernández, G., 2007a. Habitat use by immature loggerhead sea turtles in the Algerian Basin (western Mediterranean): swimming behaviour, seasonality and dispersal pattern. Marine Biology 151, 1501–1515.

Revelles, M., Isern-Fontanet, J., Cardona, L., San Félix, M., Carreras, A., Aguilar, A., 2007b. Mesoscale eddies, surface circulation and the scale of habitat selection by immature loggerhead sea turtles. Journal of Experimental Marine Biology and Ecology 247, 41–57.

Ropert-Coudert, Y., Grémillet, D., Kato, A., 2006. Swim speeds of free-ranging great cormorants. Marine Biology 149, 415–422.

Sale, A., Luschi, P., Mencacci, R., Lambardi, P., Hughes, G.R., Hays, G.C., Benvenuti, S., Papi, F., 2006. Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. Journal of Experimental Marine Biology and Ecology 328, 197–210.

Savage, R.E., 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fishery Investigations, Series 2 12, 1–88.

Schofield, G., Bishop, C.M., MacLean, G., Brown, P., Baker, M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2007. Novel GPS tracking of sea turtles as a tool for conservation management. Journal of Experimental Marine Biology and Ecology 347, 58–68.

Scott, D.W., 1979. On optimal and data-based histograms. Biometrika 66, 605–610.

Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D., 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. Journal of Animal Ecology 74, 755–761.

Smith, W.H.F., Sandwell, D.T., 1997. Global seafloor topography from satellite altimetry and ship depth soundings. Science 277, 1957–1962.

Strauss, R.E., 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108, 344–352.

Vanderploeg, H.A., Scavia, D., 1979. Two electivity indices for feeding with special reference to zooplankton grazing. Journal of the Fisheries Research Board of Canada 36, 362–365.

Watson, K.P., Granger, R.A., 1998. Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). Journal of Experimental Biology 201, 2497–2505.

Weng, K.C., Boustany, A.M., Pyle, P., D., A.S., Brown, A., Block, B.A., 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Marine Biology 152, 877–894.

Wessel, P., Smith, W.H.F., 1991. Free software helps map and display data. Eos, Transactions. American Geophysical Union 72, 441.

Wilson, R.P., Liebsch, N., 2003. Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates. Marine Biology 142, 537–547.

Wiltschko, R., Wiltschko, W., 1995. Magnetic orientation in animals. Springer-Verlag, Frankfurt, Germany.

Witherington, B., 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. Marine Biology 140, 843–853.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall Inc., New Jersey, USA. 718 pp.

Zug, G.R., Balazs, G.H., Wetherall, J.A., 1995. Growth in juvenile loggerhead sea turtles (*Caretta caretta*) in the North Pacific pelagic habitat. Copeia 1995, 484–487.